Grossman

ESSENTIALS OF PHYSIOLOGICAL PSYCHOLOGY

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Sebastian P. Grossman

DEPARTMENT OF PSYCHOLOGY
UNIVERSITY OF CHICAGO

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PREFACE

In my *Textbook of Physiological Psychology*, published in 1967, I attempted to present a fair and thorough coverage of the available experimental literature and deliberately refrained from imposing on this material conclusions and generalizations that reflected my personal biases. I have found this type of presentation useful in my own graduate level courses because it invites synopsis and evaluation by the student instead of uncritical acceptance of predigested and biased opinions. However, this approach assumes a fair degree of prior preparation and sophistication and is not, in most instances, readily adaptable to an introductory course.

The present textbook, *Essentials of Physiological Psychology*, is specifically designed to fit the needs of an introductory course in physiological psychology. It covers the subjects that were included in the earlier version but emphasizes synopsis, synthesis, explanation, and conclusion. The principal developments in each area are presented in terms of key experimental findings and their theoretical implications. No attempt is made to present an exhaustive review of the literature.

The book has four sections. Section 1 contains a brief discussion of some of the techniques used in physiological psychology; a summary of a few of the neurophysiological principles that govern the actions of nerve cells and of the brain as a whole; and an outline of the neuroanatomical information needed to find one's way through the mammalian brain. These introductory chapters are not intended to take the place of expert treatises but seek to provide a suitable introduction for the typical undergraduate or graduate student in psychology.

The second section outlines the structure and function of some of the organism's primary input and output systems. It includes chapters on visual, auditory, and chemical sensory mechanisms, which are intended to provide appreciation of the processes that translate physical changes in the environment into proportional physiological signals. The rich and complex field of perceptual phenomena and their relationship to sensory events warrants separate treatment. The chapter on motor functions discusses how the central nervous system translates changes in its own state into overt actions. The material presented in the second section serves as background information for Sections 3 and 4, which constitute the topics of primary interest. It can be skipped if the course does not provide sufficient time for adequate coverage of all segments of this book.

Section 3 contains six chapters concerned with the biological basis of basic motivational processes such as hunger, thirst, sexual arousal, affective reactions, sleep, and the organism's response to reward and punishment. The final chapter integrates the principal observations from the diverse areas into a general model for simple motivational processes. In these chapters, the principal experimental observations on which our current knowledge of the phenomena in question rests are reviewed in detail and their implications and shortcomings are discussed. An attempt is made to provide critical

synopses and to illuminate major trends and developments. Reviews and summaries are liberally used.

The fourth section is devoted to a discussion of the biological basis of learning and its end product, memory. The opening chapter presents some of the conceptual and practical problems that have made research in this important area very difficult. The following chapters discuss research and theory concerning the anatomical substrate of learning and memory; the electrophysiological, biochemical, and neuropharmacological changes that may accompany learning and/or recall; and the biochemical properties of the memory trace. The section ends with a brief discussion of the theoretical models that have been proposed to account for the functional or structural changes occurring in the nervous system as a result of learning. Many of the interpretations offered in this section are speculative because "hard" information is difficult to obtain in this area. Once again, I stress the principal developments and present frequent summaries and reviews of the often complex experimental findings.

I am deeply indebted to my wife, Lore, for her encouragement and patience during the gestation of this manuscript and to Rena Appel for her generous editorial, administrative, and clerical assistance with all phases of the manuscript. I also thank my students who, over the years, have contributed in many ways to the research and ideas presented here.

Sebastian P. Grossman

CONTENTS

SECTION 1

An Introduction to Neurophysiology and Neuroanatomy

Physiological psychologists are concerned with the physiological events which correlate with psychological processes such as affective reaction, sexual arousal, or learning. Before we can begin to discuss these complex matters, it is necessary to acquire at least a rudimentary understanding of related fields that are more specifically concerned with the structure and function of biological organisms. Since psychological processes are most directly related to the activity of the brain and associated peripheral neural pathways, we can justify concentrating on two aspects of these complex fields—neurophysiology and neuroanatomy—for the purpose of our introductory discussions. It should be clear, however, that physiological psychologists cannot ignore nonneural aspects of the organism in their work.

The first section of this book contains condensed and simplified introductions to neurophysiology and neuroanatomy as well as a very brief description of some of the techniques used to obtain information about the structure and function of the brain. These chapters are intended to provide an overview of the geography of the central nervous system and an appreciation of some of the physicochemical events that occur in it. They will make difficult reading for the nonbiologist, particularly because the ancient discipline of anatomy relies extensively on Latin terminology. It may be best to skim this material to get a feel of the land and return to it later in the context of specific substantive issues that will be raised in subsequent sections of this book.

Chapter 1

RESEARCH PROCEDURES IN PHYSIOLOGICAL PSYCHOLOGY

The physiological psychologist is concerned with the relationship between physical and chemical events in the organism (particularly in its nervous system) and resultant psychological processes such as perception, motivation, or learning. There are two principal ways to investigate this relationship experimentally. Potentially the most satisfying but also the most difficult approach is to record the physical and chemical events and directly correlate them with behavior. An approximation to this ideal state can be attained by monitoring some of the electrical changes that occur when living tissue is active. We are only learning to obtain meaningful recordings of such bioelectric phenomena, but the approach is promising. The second principal approach to the study of the relationship between physical and psychological events consists of an attempt to interfere in some way with physiological processes and note the resulting behavioral changes. Here, too, our tools are still crude, as we shall see in a moment.

RECORDING TECHNIQUES

Only few attempts have so far been made to analyze chemical reactions in the intact organism, largely because the available procedures cannot do so without interfering with the very events they are trying to measure. Instead, we have concentrated on recording the electrical potentials that are generated by nerve cells as well as nonneural tissue during excitation or inhibition.

Single-Cell Activity

The activity of single cells can be recorded by

inserting the very fine (> 0.5 micron) tip of a wire electrode into the cell or into the extracellular spaces surrrounding it. Because of the size of its tip, such an electrode has a very high electrical resistance (impedance), and special amplifiers are required to record the electrical potential that is generated whenever the cell is active. When the electrode is outside the cell, this potential consists of a very brief (less than one millisecond) spike. The amplitude of this potential varies as a function of the distance between the recording electrode and the cell that generates it but rarely exceeds 500 microvolts. Intracellularly recorded potentials are much larger (often 100 millivolts) and complex (because slow potential changes that precede and follow the spike potential can be seen). (See Figure 1–1, line *F*).

Excitatory inputs to a cell shift the membrane potential and trigger a spike discharge when a threshold of positivity is reached. Inhibitory inputs shift the membrane potential in the opposite direction and reduce the probability of a spike discharge. The shifts in membrane potential cannot be seen in extracellular recordings.

In the awake unrestrained animal the brain moves continually, and it is impossible to obtain intracellular recordings. Recent technological advances have made it possible to obtain extracellular recordings from unrestrained animals, at least for a brief period of time. This is typically accomplished by inserting somewhat larger microelectrodes (tip diameter about 5 to 10 microns) into the brain until the spike discharges of a few cells can be recorded. Since the amplitude of the extracellularly recorded spike discharge is determined by the distance between the electrode and the cell, different cells can be identified on the basis of the amplitude of the spike discharge (see Figure 1–1, line *E*). This convenient feature is also the principal factor that limits the usefulness of this technique. As the brain moves with respect to the recording electrode, the distance between the electrode and a particular cell changes, and it becomes impossible to identify the cell in terms of previously obtained records.

Multiunit Activity

Still larger electrodes are used to record the spike potential of a large number of individual cells. Electrodes with a tip diameter of about 100 microns record the activity of so many cells that it becomes impossible to identify individual cells (see Figure 1–1, line *D*). Such population recordings may be more informative than recordings of the activity of a single cell because they reflect functional changes in the activity of significant numbers of neurons. To estimate the effect of a stimulus on a functional unit of the brain, it is necessary to either record many hundreds or thousands of single units (a tedious task at best) or to obtain a multiple-unit recording that reflects the average response of the relevant population of cells.

It is customary to use an electronic filter to remove slow potential changes below about 800 cycles per second or Hertz (Hz) from the multiple unit record and then integrate the total remaining electrical activity. Theoretically, this should provide a good estimate of the direction of the response of a fairly small number of cells (perhaps a few hundred) and give us an important measure of brain activity. The principal limitation of this method arises from the fact that the functional organization of the brain does not conform very closely to geographic boundaries so that it is difficult to obtain a multiple-unit recording from a homogeneous population of cells.

Electroencephalographic Recordings

Still larger macroelectrodes (with a tip diameter of several hundred microns) are used to record the rhythmic slow potential changes that are present in the brain even in the absence of particular stimulation. These electroencephalographic (EEG) recordings are thought to be related to the spike activity of single cells, but this relationship is clearly not a simple one. Concurrent recordings of EEG and single-cell activity from the same region of the brain have not yet revealed the principles that relate the two measures. An interpretation of the EEG in terms of functional changes is therefore difficult. EEG

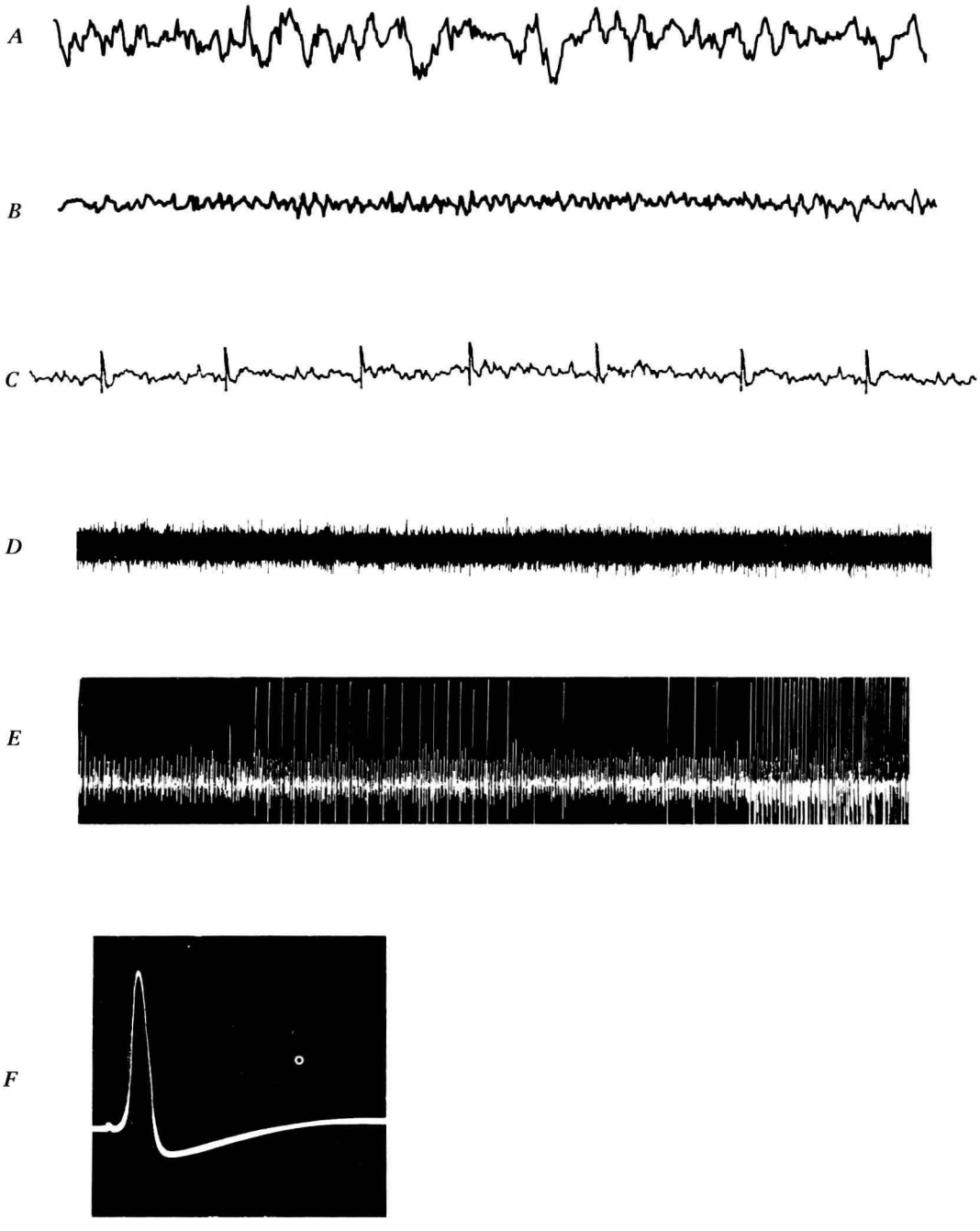

FIG. 1–1. Electrophysiological signals which are commonly recorded from the nervous system. (*A*) EEG of a quiet subject; (*B*) EEG of an aroused subject; (*C*) evoked potentials superimposed on the cortical EEG; (*D*) multiple unit activity; (*E*) single unit activity recorded extracellularly; (*F*) single unit activity recorded intracellularly. The EEG and evoked potentials are recorded from large electrodes, the single unit activity from very small microelectrodes.

recordings are nevertheless used extensively, largely because they are easily obtained even from electrodes that are attached to the surface of the skull.

During sleep or inattentive wakefulness, the EEG record is dominated by slow (6 to 12 Hz), high-amplitude (200 to 500 microvolts) rhythmic waves (see Figure 1–1, line *A*). During attentive wakefulness, a much less regular, high-frequency (up to several hundred Hz) activity appears that is of much lower amplitude (20 to 200 microvolts) (see Figure 1–1, line *B*). Largely because of this correlation with sleep and wakefulness, it is customary to assume that the rhythmic slow waves reflect synchronous cellular activity that cumulates to produce the high amplitudes. This pattern of activity is thought to characterize a state of inactivity or inhibition. The irregular high-frequency activity that is found in the waking state, on the other hand, is believed to reflect the asynchronous firing of small cell populations that cancel each other and thus produce low amplitude discharges. There is little experimental support for this popular belief and some observations (such as periods of high frequency activity during deep sleep) that contradict it.

The EEG record contains some components that can be related to specific functional events and, in some instances, cellular activity. The best example of this is the *evoked potential*, which is recorded from the sensory projection areas of the cortex following the presentation of a novel stimulus (see Figure 1–1, line *C*). These relatively large potentials have been shown to be lawfully related to the response of single cells.

Slow Potentials

Even slower potential changes can be recorded, particularly from the cortical surface of the brain when direct-coupled (D.C.) amplifiers and nonpolarizing electrodes are used. Several negative and positive potentials are often seen following the presentation of a stimulus, and the entire response may last as long as a millisecond.

Electrical Potentials in Nonneural Tissues

All tissues develop bioelectric potentials during activation, and it is possible to record these potentials from a variety of sources. Muscle tissue, for instance, develops high-amplitude (several millivolts) spike potentials that can be recorded by placing wire electrodes into or on the surface of muscle. The resulting electromyogram (EMG) is an index of muscle tension that is sometimes used to monitor sleep or "tension." The activity of heart muscle is best recorded by placing large disk electrodes on the skin of the arms and legs (thus recording the potential across the heart). The resulting electrocardiogram (EKG) is volume conducted and sufficiently large that a clear record can be obtained if other muscle activity is discouraged.

ELECTRICAL AND CHEMICAL STIMULATION

Neural as well as nonneural tissues react to brief pulses of electric current. When such current is applied to the efferent motor pathways or central representations of the motor system, movements can be elicited. We have no way of ascertaining how "normal" the response to electrical stimulation is and whether the passage of electric currents always excites rather than inhibits the tissue on which it is acting. Electrical stimulation is nevertheless commonly used and has given us some insights into the functions of the nervous system.

Typically, two small wire electrodes are inserted into the brain, and a train of brief (0.1 to 10.0 millisecond) pulses of about 10 to 100 microvolts is applied between the electrodes. The response of individual cells is all or none. An increase in the amplitude of the stimulating current therefore cannot enhance its effects on a cell that is already responding. Increases in the amplitude of the stimulating current do, however, produce a more extensive spread of the current and thus affect larger areas of the brain.

The brain does not seem to be neatly organized in such a manner that all cells that contribute to a particular function cluster in a geographically defined area. A certain amount of anatomic organization fortunately obtains, but a great deal of intermingling occurs within these gross geographic boundaries. Because the spread of electric current is determined only by structural variables, its effects are limited geographically rather than on the basis of functional considerations.

To circumvent this shortcoming of the electrical-stimulation technique, attempts have been made to obtain a more selective activation of functionally defined populations of cells by microinjections of chemicals into the brain. This approach is based on the fact that many cells, neural as well as nonneural, respond selectively to some chemical substances and that these selective affinities are often closely related to the functional role of these cells. Anyone who consumes aspirins, coffee, tranquilizers, alcohol, or any medication does so in the expectation that this is true. The psychopharmacological approach to the study of brain functions is relatively novel, but important advances have already been made.

ABLATION

The simplest way to obtain some information about the function of a part of the body is to remove it and observe the resulting behavioral and physiological changes. When applied to the nervous system, this apparently simple and direct approach often gives ambiguous answers because the behavioral and physiological effects of localized damage merely reflect the organism's ability to operate without the structure that has been destroyed rather than its functions when it is present. This seemingly minor distinction is important because the nervous system appears to be constructed such that several geographically distinct mechanisms often interact to control a particular function. There is a good deal of duplication in such a system, and the degree of "overdetermination" seems to be greater the more important the function is. The ablation procedure has nevertheless given us a great deal of information and is widely used today.

Surgical ablation procedures have been used to transect the spinal cord or brainstem, to remove major sections of the brain, or to cut particular sensory or motor pathways. More restricted damage to surface portions of the brain are made by aspiration. Most current investigations are concerned with the effects of restricted damage to deep structures. These lesions are most easily made by passing a fairly strong (1 to 4 milliamperes) direct current through two implanted wire electrodes. This produces electrolytic reactions in the path of the current flow, which destroy the tissues. An alternative procedure uses high-frequency alternating current, which destroys by heating and is less likely to result in a transient stimulation of the tissues that surround the lesion.

Lesion procedures have two major drawbacks: (1) the effects of a lesion, like those of electrical stimulation, are geographically limited so that a selective effect on functionally defined pathways is difficult to achieve; (2) once the damage is done, it is impossible to obtain a sample of the organism's "normal" behavior—the effects are irreversible.

Pharmacological techniques have recently been developed that attempt to circumvent one or both of these objections. A reversible inhibition of cortical functions can be obtained by topical applications of potassium chloride. A reversible blockade of subcortical mechanisms may be obtained by microinjections of drugs, such as procaine, that temporarily interfere with neural functions. A more functionally selective blockade can be obtained by microinjections of drugs that selectively interfere with the transmission of information between some nerve cells.

STEREOTAXIC PROCEDURES

In order to place electrodes for recording, stimulation, or lesioning in specific parts of

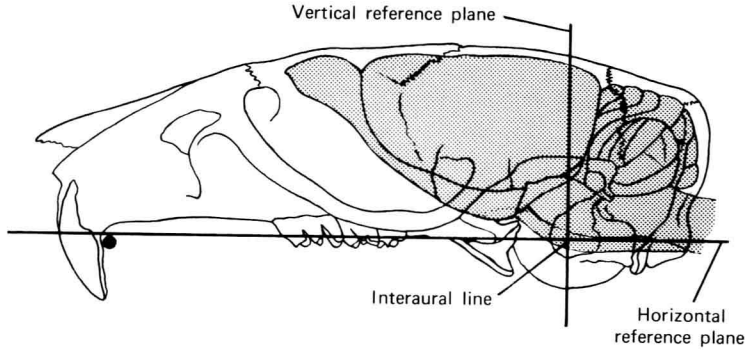

FIG. 1–2. Rat brain (shaded area) inside skull, showing the location of the commonly used reference points for stereotaxic surgery. The horizontal plane is an imaginary line extending from the external meatus of the ear to a point just behind the large incisor teeth, which are used to fix the animal's head in the stereotaxic instrument. The vertical reference plane is a line perpendicular to the first. It is customary to use an imaginary line between the external meatus of the two ears (the interaural line) as a convenient zero point for these two planes, and the middle of that line as a zero point for the lateral dimension. Any point in the brain can then be described as being some distance anterior or posterior to the interaural line, some distance above or below it, and some distance lateral to the center of it. The animal's head is fixed in the stereotaxic instrument such that the exact location of the interaural line and the slope of the horizontal line (and the slope of the vertical line) are known. It thus becomes possible to place the tip of an electrode precisely at a specified point in the brain without removing the tissues covering it.

the brain, a system of coordinates has been developed that permits the localization of each point in the brain in three planes. By recording the extent and location of each anatomical subdivision of the central nervous system, an "atlas" has been constructed that locates each structure with respect to these planes which, in turn, are related to some constant landmark such as the imaginary line that connects the ears, or a plane perpendicular to the top of the skull. Each structure can then be identified as being x millimeters above landmark A; x millimeters ahead of landmark B; and x millimeters to the side of landmark C (see Figure 1–2).

The stereotaxic machine is simply a metal frame that fixes the position of the head with respect to these landmarks and is calibrated such that the electrode holder can be placed accurately with respect to them. The surgical procedure is not difficult (see Figure 1–3). Once a set of coordinates has been selected from the atlas, an electrode is inserted into the electrode holder such that its tip has a known relationship to the three basic landmarks of the head in the stereotaxic instrument. The experimental animal is then anesthetized and its head fixed, by a system of clamps, in the stereotaxic instrument. Next, a small incision is made in the skin of the top of the head and a hole drilled through a point that has been fixed on the basis of the atlas coordinates. The wire electrodes are then inserted into the brain to the depth of the structure under investigation. The electrodes are fastened to the skull by a bit of dental cement, the incision is closed, and the animal is ready for stimulation or lesioning following a few days of postsurgical recuperation. Cannulas that permit injections of drugs into the brain are implanted in exactly the same way.

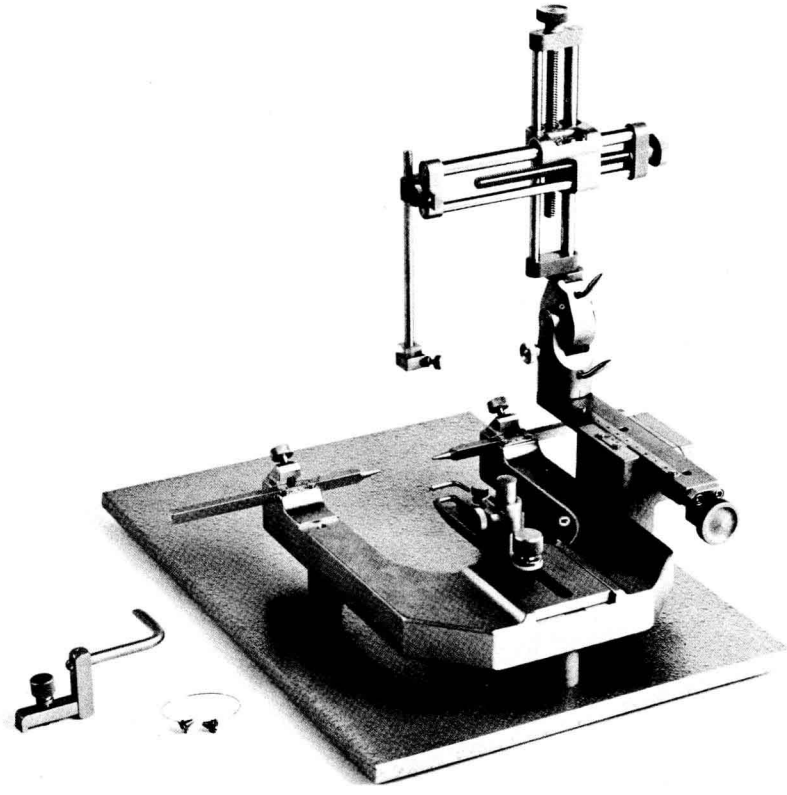

FIG. 1–3. Stereotaxic instrument for small rodents. The animal's incisor teeth are placed into the opening in the holder, which is affixed to the center of the front of the instrument. The small clamp is then lowered until it grips the animal's nose. The two ear bars are inserted into the external meatus of each ear. This establishes the three reference points discussed in Fig. 1–2. An electrode can then be placed into the movable carrier mounted on one side of the stereotaxic apparatus and the position of this carrier can be adjusted to permit accurate placement of the electrode into any portion of the brain.

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ANATOMICAL PROCEDURES

Regardless of how one investigates the functions of the nervous system and its relationship to behavior, it is essential to determine precisely where the electrodes, lesions, or cannulas were placed. In some instances, it is sufficient to perfuse the brain with some hardening agent and to perform a gross dissection. More typically, it is necessary to analyze the affected region microscopically. A variety of anatomical procedures are available for this purpose.

In most cases, the brain tissue is hardened by perfusing it with some agent, such as formaline, and freezing it or embedding it in some gradually hardening substance, such as paraffin. The brain can then be cut into very thin (5 to 50 microns) slices, much as one would slice a salami. By a careful adjustment of the *microtome* that is used to perform this task, one can arrange the angles of this cut such that the slices duplicate the pattern of the stereotaxic atlas. The thin sections of brain tissue are then briefly submerged in various dyes that selectively stain cell bodies, or axons, or only abnormal tissues that have degenerated because of damage. The sections are then dried and mounted on glass slides

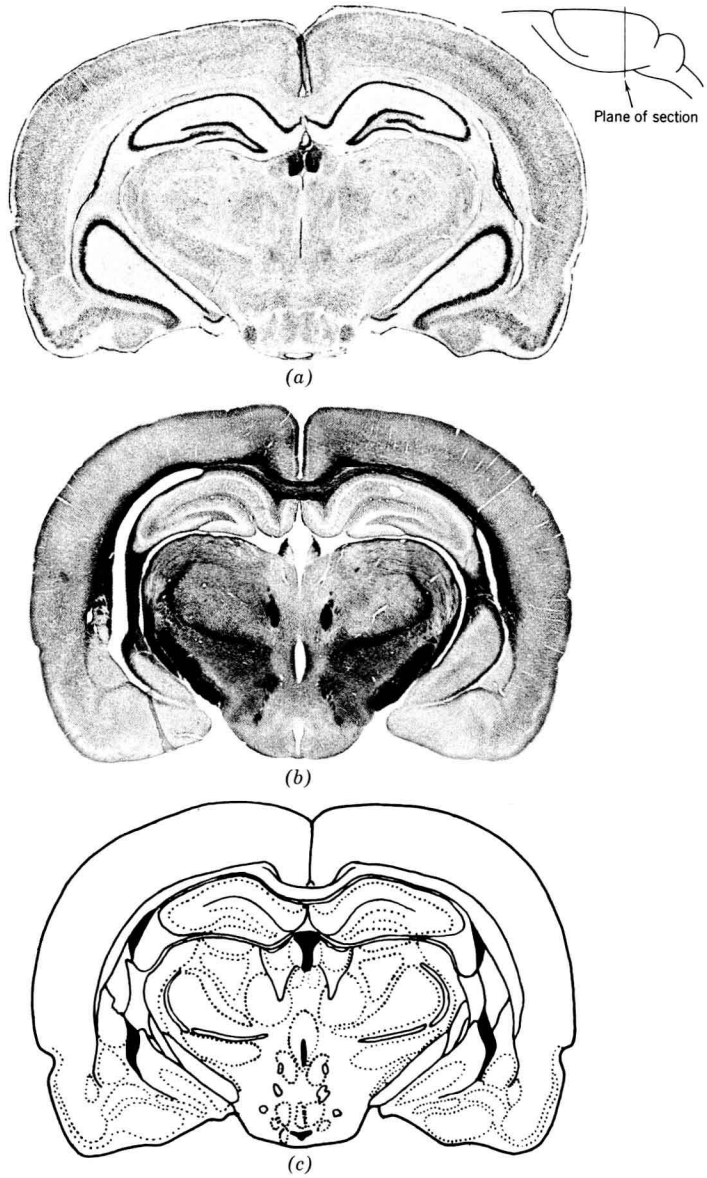

FIG. 1–4. A cross sectional "slice" of the rat brain at a point shown in the insert. (*a*) was exposed to a dye that selectively darkens the *bodies* of nerve cells. (*b*) was exposed to a dye that stains nerve *fibers* black. (*c*) is a corresponding section from a stereotaxic atlas giving the vertical coordinates on the sides and the lateral coordinates on the top and bottom. The notation in the lower right-hand corner indicates that this slice is 3.5 mm anterior to the interaural line.

(After *A stereotaxic atlas of the developing rat brain* by Nancy Sherwood and P. Timiras. Copyright © 1970. Originally published by the University of California Press; reprinted by permission of The Regents of the University of California.)

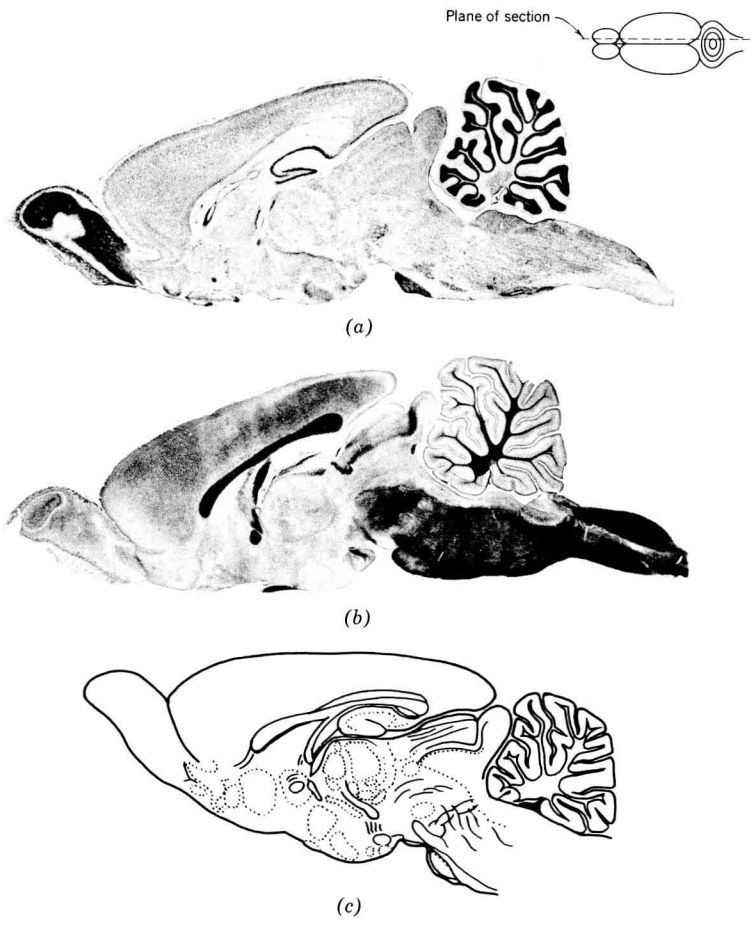

FIG. 1–5. Longitudinal (parasagittal) slice of the rat brain at a point indicated on the insert at top. (*a*) was exposed to a dye that selectively darkens the *bodies* of nerve cells. (*b*) was exposed to a dye that stains nerve *fibers* black. (*c*) is a corresponding section from a stereotaxic atlas (simplified) giving the vertical coordinates on the sides and the anterior-posterior coordinates at the top and bottom. The notation in the right-hand corner indicates that this slice is 1 mm from the center of the interaural line.

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and are ready for microscopic analysis. If everything was done just right, the localization of the electrode or lesion is easily performed by comparing the histological materials with the corresponding sections of the stereotaxic atlas (see Figures 1–4 and 1–5).

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